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RESEARCH ARTICLE

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Differences in novel food response between *Pongo* and *Pan*

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The diversity of great ape diets requires behavioral flexibility. Consequently, the exploration of potentially novel food sources is supposedly beneficial, but simultaneously, apes show high neophobia to prevent harmful and poisonous food intake. Social information, such as presence of group members or observations of non-naïve, experienced individuals have been demonstrated to affect the acceptance of novel food items in primates. Sociality may have evolutionary effects on the response of apes to novel foods. Here we assess the *social information hypothesis*, which predicts that selection favors higher neophobia in species where social information is abundant. We report the results from 134 great apes housed in multiple facilities from four closely related species that naturally differ in their degree of sociality: *Pongo pygmaeus*, *Pongo abelii*, *Pan troglodytes* and *Pan paniscus*. We examined individuals' reactions to novel foods when alone, which enabled us to detect any inherent differences and revealed significant distinctions between species. Chimpanzees and bonobos, that are naturally exposed to higher amounts of social information, were less likely to consume novel foods alone (showed higher neophobia) than the two more solitary orangutan species. Chimpanzees were especially cautious and showed higher explorative behaviors before tasting novel food than other species. Age influenced neophobia as younger individuals of all species took longer to taste novel foods than adults did.

KEYWORDS
great apes, neophobia, novel food, sociality, social information

1 | INTRODUCTION

Great apes need a diverse diet to meet nutritional needs and thus have evolved to be innovative and behaviorally flexible (Deaner, Isler, Burkart, & van Schaik, 2007; Reader, Hager, & Laland, 2011). Innovativeness is often measured in terms of integration of new food items or foraging techniques into the behavioral repertoire (Biro et al., 2003; Kummer & Goodall, 1985; Nishida, Matsusaka, & McGrew, 2009; Russon et al., 2009; van Schaik, van Noordwijk, & Wich, 2006). Yet, few studies have focused on the different pathways leading to innovations, diet expansion and how great apes react to novel foods (Bastian et al., 2010; Biro et al., 2003; Boesch, 1995; Kummer & Goodall, 1985; Manrique, Völter & Call, 2013; Ramsey, Bastian & van Schaik, 2007; Russon et al., 2009). Even fewer studies have been conducted in a comparative framework (but see also: Gustafsson, Saint Jalme, Bomsel, & Krief, 2014). Interspecific comparisons of novel food response can contribute to our understanding of how innovative species—like the great apes—overcome food neophobia and incorporate new foods in their diets.

Due to the seasonality of their habitats, their extractive foraging behaviors, and high reliance on fallback foods, great apes have developed a broad and variable diet. How such species react to novelty is of great interest as they are exposed to the well-described "*omnivorous dilemma*" (Greenberg, 2003; Rozin, 1977). The omnivorous dilemma predicts that species with the ecological characteristics described above, depend on maintaining a balance between *food neophobia*, as a protection mechanism against harmful food intake and a *tendency to explore novel foods* to adopt the species-specific diet but also to flexibly adjust to changing conditions.

Ecological influences, such as habitat risk and feeding niche can explain why many closely related bird species differ in their levels of neophobia and exploration tendency (Mettke-Hofmann, 2014; Webster & Lefebvre, 2001). Accordingly, in a study that compared two primate species, differences in novel object exploration between geladas (*Theropithecus gelada*) and chacma baboons (*Papio ursinus*) were attributed to dietary differences. The omnivorous baboons showed a higher exploration tendency towards novel objects than the grass specialized geladas (Bergman & Kitchen, 2009). In the case of gorillas (*Gorilla gorilla*), a plant-based, high-fiber diet combined with a high digestive tolerance of secondary compounds, may allow lowered neophobia compared to other apes (Gustafsson et al., 2014; Remis, 2003; Remis & Kerr, 2002). Apart from the heavily vegetation based diet of gorillas (Doran-Sheehy et al., 2009), all great ape species have highly diverse diets and yet paradoxically show rather high neophobia, especially in their natural habitats (Call, 2017; Forss, Schuppli, Haiden, Zweifel, & van Schaik, 2015; Matsuzawa & Yamakoshi, 1996; Takahata, Hiraiwa-Hasegawa, Takasaki, & Nyundo, 1986; Takasaki, 1983).

While wild apes need to be cautious and avoid potentially harmful novel items, their captive conspecifics show lower neophobia—apparently due to reduced habitat risks (Forss et al., 2015; Kummer & Goodall, 1985; van Schaik et al., 2016). In addition, captive great apes also show increased curiosity, which encourages interactions with novel items, due to human oriented social relationships (Damerius, Graber, Willems, & van Schaik, 2017).

The balanced relationship between *cautiousness* (high neophobia) and *curiosity* (high exploration tendency) in primates is likely influenced by multiple factors such as the type of novel food, for example, sugary or bitter (Gustafsson et al., 2014; Johnson, 2007; Yamakoshi, Hirata, & Matsuzawa, 2002), repeatable exposure to novelty (Visalberghi, Valente, & Fragaszy, 1998), taste perception (Steiner and Glaser, 1984; Steiner, Glaser, Hawilo, & Berridge, 2001) and social influences (Ueno & Matsuzawa, 2005; Visalberghi & Addessi, 2000; Visalberghi & Fragaszy, 1995; Voelkl, Schrauf, & Huber, 2006; Yamamoto & Lopes, 2004). As primates learn what to eat and what not, taste perception provides useful feedback against, for example, bitter food items that can potentially contain toxic secondary compounds (Remis, 2003, 2006; Steiner & Glaser, 1984; Steiner et al., 2001). However, *prior* to tasting a potential novel food item, an individual cannot initially know its harmfulness, and neither are all poisonous substances detectable through taste feedback (Hladik & Simmen, 1996) nor do all primates avoid them. Captive chimpanzees lick nuts even when covered with the bitter substance Bitrex (Tennie pers. observation.) and wild chimpanzees at Budongo, Uganda have been reported to consume bitter tasting seeds (Reynolds et al., 1998).

Given that misjudgment comes at (potentially) high costs, primates may not primarily rely solely on taste perception but also use additional cues of *social* information provided by experienced conspecifics (Boyd & Richerson, 1985; Giraldeau, 1997; Laland, 2004). Multiple studies have experimentally demonstrated that social factors increase novel food acceptance in various primate species: marmosets (*Callithrix jacchus*) (Voelkl et al., 2006; Yamamoto & Lopes, 2004), capuchin monkeys (*Cebus apella*) (Visalberghi & Addessi, 2000; Visalberghi & Fragaszy, 1995) and chimpanzees (*Pan troglodytes*) (Gustafsson et al., 2014; Ueno & Matsuzawa, 2005). While these results illustrate the influence of social factors when an individual encounters a novel food item, no study so far has addressed this influence from a *phylogenetic perspective*. In other words, whether closely related species with different levels of sociality, differ in their response to novel foods.

The *social information hypothesis* predicts that species that use social cues when learning their diet composition, evolve a higher intrinsic neophobia towards novel foods prioritizing the use of safe social information before risky individual exploration (Forss, Koski, & van Schaik, 2017; Giraldeau, 1997; Laland, 2004). If this is the case, one would expect group living species with a highly social lifestyle to have evolved higher intrinsic neophobia than closely related solitary species, which can rely less frequently on the presence of a social information source. In this study we focused on addressing this phylogenetic viewpoint of the *social information hypothesis* in four great ape species: Bornean orangutans (*Pongo pygmaeus*), Sumatran orangutans (*Pongo abelii*), chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*).

The selected great ape species are ideal for this comparison as they all face the "*omnivorous dilemma*" and in the wild all of them are exposed to habitat seasonality and opportunistic foraging situations (McGrew, Marchant, & Nishida, 1996; Robson, van Schaik, & Hawkes, 2006; van Woerden, Willems, van Schaik, & Isler, 2012). Apart from some intra-population variation in gregariousness in the Sumatran species (van Schaik, Fox, & Sitompul, 1996), orangutans are in general solitary species which spend most of their post-weaning time alone or in temporary small parties (Husson et al., 2009; van Schaik, 1999; van Schaik & van Hooff, 1996). Chimpanzees and bonobos on the other hand, live in fission-fusion communities where party sizes in general are larger and live in closer proximity than orangutans (Boesch & Boesch-Achermann, 2000; Chapman, White, & Wrangham, 1994; Goodall, 1986; Nishida, 1968). Party size in chimpanzees and bonobos can also differ geographically, from small party size in Western chimpanzees to large groups found in Eastern chimpanzees (Gruber & Clay, 2016). Despite this variability, parties are believed to be both larger and more stable in bonobos than in chimpanzees (Furuichi, 2009; Kano, 1982; Kuroda, 1979). Until weaning age, immatures of all four species (both orangutans, bonobos and chimpanzees) have a stable social source due to their long dependence on the mother. However, when naïve individuals start to explore their habitat more independently as adolescents, these species vary in the abundance of social information due to the differences in social life.

We tested the reactions of four great ape species (both *Pan* and *Pongo*) to novel food in multiple facilities in Europe and Africa. Due to the effect of captivity, all four species are likely less neophobic in the testing facilities than they would be in their natural habitat (Damerius et al., 2017; Forss et al., 2015). However, we were interested in whether there were any detectable predispositions in novel food response when living and tested under close to similar (here: captive) conditions. To identify any *intrinsic* differences between species, we tested the apes alone (without conspecifics present) to rule out any effect of social facilitation. Solitary testing also allowed us to evaluate separately individuals from different age classes without sources of social information being present. All individuals were exposed to a single encounter with two novel food items.

2 | METHODS

2.1 | Subjects and experimental set up

We collected data on reactions to novel foods on a total of 134 great ape subjects. To ensure a variable and representative sample, the data were collected at 13 different facilities: one wildlife sanctuary and 12 zoological gardens (Table 1). The 134 subjects ranged from 3.5 to 66 years old and belonged to four different great ape species: 21 Bornean orangutans (*Pongo pygmaeus*), 21 Sumatran orangutans (*Pongo abelii*), 23 bonobos (*Pan paniscus*) and 69 chimpanzees (*Pan troglodytes*). The data on bonobos and chimpanzees were collected between April 2017 and March 2018 and then added to an already existing data set from both orangutan species collected between 2012 and 2015 (Forss, Willems, Call, & van Schaik, 2016). All apes were housed in conspecific peer groups and were fed according to their daily routine on testing days. Therefore, individuals were neither food deprived nor especially hungry during tests.

We tested all 134 subjects on their reactions to novel foods consisting of a pile of blue colored pre-prepared potato mash topped with black olives (Figure 1). This novel food was chosen as it had already been tested with orangutans (Forss et al., 2016) and thus would allow us to expand the data set for comparative purposes by using the exact same items and methods with bonobos and chimpanzees. The blue colored potato mash was neutral and probably tasteless to the apes but visually novel and dissimilar to the natural colors of fruits and vegetables familiar to the apes. The pre-prepared potato mash was not used as food for the apes in any of the facilities where we tested our subjects (pers. comm. from the animal caretakers at each facility). The black olives represented a novel taste unfamiliar to all subjects in the study and contributed bitterness, disliked by many primates (Masi et al., 2013; Yang & Shi, 2017). As a control condition, we also tested the subjects' reactions to a familiar food item (a fruit indicated by the respective testing facility). To control for otherwise possible social facilitation (Visalberghi & Addessi, 2000; Visalberghi & Fragaszy, 1995) effect, we tested all subjects alone (solitary condition), with a few exceptions of non-separable individuals ($N = 4$), in which case we only used the data from the subject who *first* reacted to the novel food item. The total test duration was two minutes and all tests were video recorded with a SONY Handycam model HDR-CX200E. From the videos following behavioral reactions to the novel food items the following variables were coded: taste novel food (Yes/No), consume blue potato mash (Yes/No), consume black olives (Yes/No), whether or not a subject would sniff/ smell the novel food before putting it to its mouth (Yes/No), number of physical explorative actions (sniffing, touching, poking with stick) of the novel food and the latency (seconds) to taste novel food (starting from the moment the subject was one meter away from the novel food).

To test for a social facilitation effect, we additionally performed group experiments with a subsample of chimpanzees. At one zoological garden (Leintalzoo) as well as at the Ngamba Island chimpanzee sanctuary, we provided five different groups (sizes ranging from four to seven individuals) with the novel food and recorded their reactions in the same way described above. These data were then compared to the same chimpanzees' reactions from the

TABLE 1 Overview of study facilities

Facility	Species	# of subjects	Data collection dates	Age range
Allwetterzoo Münster	*Pongo pygmaeus*	6	May 2013	6–43
Apenheul Primate Park	*Pongo pygmaeus*	8	January- February 2014	13–52
Basel Zoo	*Pongo abelii*	4	November 2013	5–13
Basel Zoo	*Pan troglodytes*	7	March 2018	3,5–42,5
Berlin Zoo	*Pan paniscus*	3	August 2017	8–36
Blackpool Zoo	*Pongo pygmaeus*	3	January 2015	13–31
Dortmund Zoo	*Pongo abelii*	5	November 2012	5–19
Durrell Wildlife Conservation Trust	*Pongo abelii*	5	March 2013	9–49
Frankfurt Zoo	*Pan paniscus*	11	June 2017	7,5–66
Leintal Zoo	*Pan troglodytes*	21	September 2017	7–46
Ngamba island chimpanzee sanctuary	*Pan troglodytes*	40	September-October 2017	8–33
Paignton Zoo	*Pongo pygmaeus*	3	February 2015	18–20
Anynomous Zoo	*Pongo pygmaeus*	2	January 2013	14 & 36
Wolfgang Köhler Primate Center	*Pan paniscus*	9	April 2017	4–35,5
Wolfgang Köhler Primate Center	*Pongo abelii*	7	March 2014	4–25

FIGURE 1 Novel food items: Blue colored potato mash topped with black olives

solitary condition. As the chimpanzees tested in groups were already familiar with the blue potato mash from the individual testing condition, we used pink colored cooked spaghetti bundles as the novel food item. Spaghetti had never been served previously to the participating subjects and represented a novel texture as well as taste (pers. comm. from animal caretakers at each facility). At the same time spaghetti was equivalent in smell and tastelessness as the potato mash described above. Multiple bundles of spaghetti were placed just outside the enclosure mesh in the absence of the chimpanzees, who then were let in as a group. The group test was also video recorded, and the following measurements were taken for each subject from the video recording: taste novel food (Yes/No) and latency (seconds) to taste novel food.

2.2 | Statistical analysis

We performed all tests using R (version 3.3.3, R Core Team, 2017) and RStudio (version 1.1.383). Prior to fitting all models, we checked the distribution of the covariates as well as the number of responses per level of factor to ensure these were balanced. We z-transformed covariates to a mean of zero and standard deviation of one to facilitate the interpretation of the coefficient estimates (Schielzeth, 2010). All model estimates can be found in the Supplementary material 1 and the model stability plots can be found in the Supplementary material 2.

2.2.1 | Tasting and consumption of novel foods

We used McNemar's tests to examine if there was a difference within species in the frequency of consuming familiar foods and unfamiliar foods (blue potato mash and olives), as these were paired dichotomous variables.

We used Generalized Linear Mixed Models (GLMM: Baayen, 2008) with binomial error structure and logit link function to study which factors influenced the probability of consuming a novel food (model a). Factors included as random slopes (sex.code) were a priori manually dummy coded and centered. We included the random slopes of sex and age within facility but not the correlation between the random slopes and the random intercepts (Barr, Levy, Scheepers & Tily, 2013). To determine if the variables included had a significant effect on the response, we used a full-null model comparison lacking the fixed effects test predictors (Forstmeier & Schielzeth, 2011) using a likelihood ratio test (Dobson & Barnett, 2008). Due to convergence problems derived from the complete separation of one of the levels of the test predictors, we opted for replacing all the ones in the response by a zero, one at a time, and then average the results (code for this analysis was provided by Roger Mundry following Goodale, Ratnayake & Kotagama, 2014). Collinearity was tested calculating Variance Inflation Factors (VIF) using a linear model excluding random effects using the R function vif. No collinearity (VIF lower than 1.6 for all predictors; Fox & Weisberg, 2011) or overdispersion (0.63) issues were found. The model was fit with the R package lme4 (version 1.1–15) with the optimizer “bobyqa” and number of iterations set at 10^6.

We used Generalized Linear Models (GLM) with binomial error structure and logit link function (Lee & Nelder, 1998) to model the potential differences between species in the probability of consuming a particular food (model b: Familiar food, model c: Blue potato mash and model d: Olives). We examined the stability of the models employing different model diagnostics (leverage and DFBetas: estimated coefficients resulting from case-wise deletions), without finding any issues. To determine if the predictor as a whole influenced the response, we compared the full model to the null model (including only the intercept, Forstmeier & Schielzeth, 2011) using a likelihood ratio test (test “Chisq” in the R function anova).

2.2.2 | Novel food: exploration behavior

We also used GLM with binomial error structure and logit link function (McCullagh & Nelder 1989) to study if there were differences among species in the probability of sniffing novel food before consuming it (model e) and a GLM with poisson error structure and a log link function to study if there was an effect of species in the number of exploratory events performed before eating a novel food (model f). We examined the stability of the model in terms of leverage (model e: 0.3, threshold = 0.14; model f: 0.28, threshold 0.13), collinearity (model e: all VIF values lower than 1.12; model f: VIF of 1.08 for all predictors) and DFBetas. The leverage value indicates that there is a *potentially* high influence of some values on the data set. To determine the effect of species on the response we performed a full-null model comparison using a likelihood ratio test as described for models a, b and c. Two-sided Fisher's exact tests were used as post-hoc tests to compare the probability of sniffing between species and to compare chimpanzees and bonobos with the orangutan species in terms of exploratory events.

2.2.3 | Latency to taste novel food

We used a linear mixed model (LMM) to test whether the latency to taste a novel food was affected by age class (model g). We checked the distribution of the response and after finding out that it was heavily left skewed we performed a successful log transformation that led to an approximately normal distribution. Sex was included as a random slope within facility but not the correlation between the random slope and random intercept terms, as it was found that these were correlated (Barr et al., 2013; Schielzeth & Forstmeier, 2008). Factors included as random slopes were a priori manually dummy coded and centered (sex. code). We visually inspected the distribution of the residuals, which approached normality, and the residuals plotted against the fitted values (see Supplementary material 2). We visually evaluated the distribution of the random effects, which approached normality. DFBeta values suggested that there might be potential influential cases. All VIF values were smaller than 1.12, therefore no collinearity issues were found. The effect of age class on the response was assed performing a full-null model (omitting random effects) comparison using a likelihood ratio test as described for model d. We fitted the models using a maximum likelihood test instead of a restricted maximum likelihood (Bolker et al., 2009).

2.2.4 | Group versus solitary condition

The subjects for the follow tests were the same chimpanzees that had been tested either in single housing or in group housing, but not in both conditions, as these chimpanzees invariably consumed the novel food in the group condition (had only one level of the binomial variable).

We used GLM with binomial error structure and logit link function (McCullagh & Nelder, 1989) to assess if group housed chimpanzees differed from single housed chimpanzees in their probability of consuming a novel food (model h). To determine the stability of the model we calculated VIF obtaining values lower that 2.1 for all predictors. Thus, collinearity was not an issue. We also calculated the leverage (0.71), which was found to be above the threshold (0.28) suggesting the presence of *potentially* high influential cases. We also calculated DFBeta values, finding no obvious problems. To determine if housing conditions had an effect on the probability of consuming novel food, we performed a full-null model comparison as described for models a, b, c, and e.

We used a lineal model to analyze whether the housing condition (single or group housing) influenced the latency to taste novel food. We checked the distribution of the response and after finding out that it was heavily left skewed we performed a successful log transformation that led to an approximately normal distribution. We assessed the model stability by calculating the VIF values as described above. No collinearity issues were found. We also obtained leverage measures, which turned out to be high (0.84) and above the threshold (0.38). DFBeta values were calculated and no issues were found. DFfits were calculating finding one value higher than 2. These diagnostic measures suggest that there are values with strong leverage. A QQ plot of the residuals suggested that large values seem to be too large. No obvious pattern was observed when the fitted values were plotted against the residuals. The residuals showed a slightly left skewed distribution. The effect of the test predictor on the response was assessed using the function drop1 for predictor-wise deletions setting the test argument to "F."

3 | RESULTS

3.1 | Tasting and consumption of novel foods

We found that all species except Bornean orangutans, were more likely to consume familiar food than the novel blue potato mash ($X^2 = 14.877$, df = 3, $p = 0.002$, model a, Tables 2 and 3) and that bonobos and chimpanzees, but not the orangutan species, were more likely to consume familiar food than black olives (Table 3). In the control condition we found no species differences in the probability of consuming a familiar food (likelihood ratio test, $X^2 = 2.913$, df = 3, $p = 0.405$, model b, Table 2).

Species differed however in the probability of consuming the blue potato mash (likelihood ratio test, $X^2 = 11.78$, df = 2, $p = 0.008$, model c, Table 2, Figure 2). Post-hoc tests were conducted by repeating the model fitting changing the reference category. These tests showed that bonobos were the least likely to consume the blue potato mash and that they differed significantly from both orangutan species (bonobos-Bornean orangutans: $X^2 = 2.51$, $p = 0.01$; bonobos-Sumatran orangutans: $X^2 = 2.11$, $p = 0.04$, Figure 2). The same was true for chimpanzees, who were also less likely to consume the blue potato mash than both orangutan species (chimpanzees-Bornean orangutans: $X^2 = -2.48$, $p = 0.01$; chimpanzees-Sumatran orangutans: $X^2 = -2.02$, $p = 0.04$, Figure 2). Chimpanzees did not differ significantly from bonobos (chimpanzees-bonobos: $X^2 = 0.54$, $p = 0.59$, Figure 2) and the two orangutan species did not differ significantly from each other (Sumatran orangutans-Bornean orangutans: $X^2 = -0.44$, $p = 0.66$, Figure 2).

Species, as a whole, differed in the probability of consuming olives (likelihood ratio test, $X^2 = 11.37$, df = 3, $p = 0.01$, model d, Table 2, Figure 3). Post-hoc tests revealed that the only significant differences in the probability of consuming olives were between bonobos and both orangutan species (bonobos-Bornean orangutans: $X^2 = -2.76$, $p = 0.01$; Bonobos-Sumatran orangutans: $X^2 = -2.66$, $p = 0.01$, Figure 3).

3.2 | Novel food: Exploration behavior

We analyzed in detail the behavior of each subject as they first explored the novel foods *before* tasting it. Species differed significantly in the probability of sniffing (likelihood ratio test, $X^2 = 34.21$, df = 4, $p < 0.001$; model e, Table 2, Figure 4). Post-hoc Fisher's tests revealed that chimpanzees were significantly more likely to sniff than the other species (chimpanzees-bonobos: odds ratio = 3.73, $CI_{95\%} = 0.95–16.49$, $p = 0.035$; chimpanzees-Bornean orangutans: odds ratio = 19.26, $CI_{95\%} = 3.95–189.00$, $p < 0.01$; chimpanzees-Sumatran orangutans: odds ratio = 0.09, $CI_{95\%} = 0.015–0.38$, $p < 0.001$, Figure 4). Bonobos

TABLE 2 Overview of the statistical models used. Terms in bold correspond to the test predictors in each model

Model	Model structure	Sample size
a	glmer(Taste.Novel.Food~Species+Sex+z.Age+z.Age^2+(1+Sex.coded+z.Age||Facility), data, family = binomial)	134
b	glm(Consume.Familiar.Food~Species,data, family = binomial)	127
c	glm(Consume.Blue.Potato.Mash~Species,data, family = binomial)	134
d	glm(Consume.Olives~Species, data, family = binomial)	134
e	glm(Sniff.Before.Taste~Species+ z.Age+Age^2+Sex, data, family = binomial)	107
f	glm(N. Exploratory.Events.Before.Taste~Species+Sex+z.Age, data, family=poisson)	106
g	lmer(Latency.Taste.Novel.Food~ AgeClass+Sex+Species+(1+Sex.coded||Facility), data, REML = F)	105
h	glm(Consume.Novel.Food~Testing.Condition+Sex+ z.Age+z.Age^2 +Facility, data, family=binomial)	63, 3 facilities
i	lm(Latency.Taste.Novel.Food~Testing.Condition+Sex+ z.Age+z.Age^2+Facility, data)	48, 3 facilities

did not differ significantly from the orangutan species (bonobos-Bornean orangutans: odds ratio = 0.35, $CI_{95\%} = 0.04–2.29$, $p = 0.24$; bonobos-Sumatran orangutans: odds ratio = 0.35, $CI_{95\%} = 0.04–2.29$, $p = 0.24$, Figure 4). Orangutan species did not differ in the probability of sniffing (Bornean orangutans-Sumatran orangutans: odds ratio = 1.76, $CI_{95\%} = 0.18–23.49$, $p = 0.65$, Figure 4).

In line with the differences in sniffing behaviors, we also found that great ape species differed in the amount of exploratory actions performed before tasting a novel food ($X = 10.55$, df = 3, $p = 0.01$, model f, Table 2, Figure 5). Post-hoc Fisher's test revealed that chimpanzees differed significantly from both orangutan species (chimpanzees-Bornean orangutans: $p < 0.001$, chimpanzees-Sumatran orangutans: $p = 0.01$, Figure 5) but that none of the other species significantly differ in the amount of exploratory actions.

3.3 | Latency to taste novel food

Out of those subjects' that *did taste* the novel foods, we found that there was a significant difference between age classes regarding how fast subjects tasted novel food (likelihood ratio test, $X^2 = 10.47$, df = 2, $p = 0.005$, model g, Table 2, Figure 6). Adult subjects (11–40 years) were faster in tasting novel foods than both immatures (0–10 years) and older adults (>40 years). As many of the bonobos and chimpanzees did not taste the novel food items at all, those subjects could not enter this analysis. Consequently, the sample size of different ages was uneven and smaller within each species, which is why we used age classes to achieve a more balanced distribution.

3.4 | Group versus solitary condition

Chimpanzees that were tested in either a group or a solitary situation were compared in terms of their probabilities of consuming novel food. In the groups chimpanzees had a significantly higher probability of consuming novel food than those that were solitary (likelihood ratio test, $X^2 = 3.89$, df = 1, $p = 0.046$, model h, Table 2, Figure 7). This model also revealed the existence of significant differences between facilities (likelihood ratio test, $X^2 = 11.12$, df = 2, $p = 0.004$, Figure 7).

When the latency of tasting the novel food was compared between the two testing conditions, chimpanzees in groups were significantly faster than chimpanzees in the single condition ($F = 2.72$, $p = 0.03$, model i, Table 2, and Figure 8).

4 | DISCUSSION

Our findings support the *social information hypothesis*, which predicts reliance on social cues to have an evolutionary effect by selecting for higher intrinsic neophobia in species where social information is abundant (Forss et al., 2017). Previous studies have shown that the presence of a conspecific can help primates overcome food neophobia (Visalberghi & Addessi, 2000; Visalberghi & Fragaszy, 1995; Voelkl et al., 2006; Yamamoto & Lopes, 2004). Individuals of the two solitary orangutan species were more inclined to taste and consume novel foods than individuals of the two community living species—chimpanzees and bonobos (Figures 2 and 3). Abundance of social information differs when individuals of the four tested ape species

TABLE 3 Frequencies of food consumption of each species and results from the McNemar within species comparisons of the probabilities of consuming novel foods (blue potato mash (BMS) and olives (OS)) with the probabilities of consuming a familiar food (Fam)

		Blue potato mash—Familiar food			Olives—Familiar food		
Species	FreqFam	FreqBMS	χ^2 BMS	p	FreqOS	χ^2 OS	p
Bonobo	0.957	0.391	11.077	0.001	0.348	12.071	0.001
Bornean orangutan	0.909	0.773	0.8	0.371	0.773	0.8	0.371
Chimpanzee	0.967	0.456	26.036	0	0.588	15.429	0
Sumatran orangutan	1	0.714	4.167	0.041	0.762	3.2	0.074

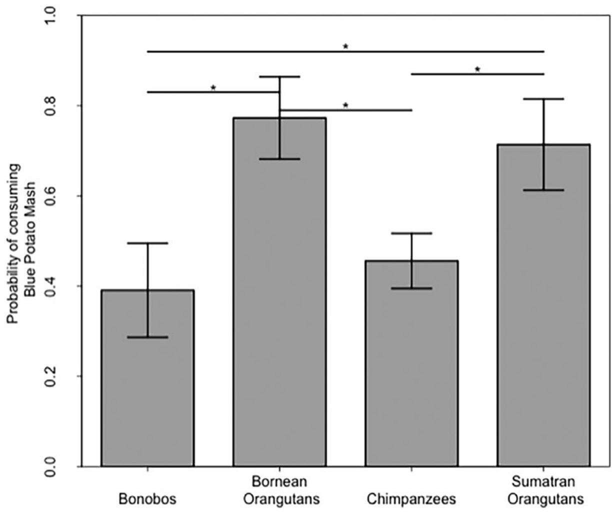

FIGURE 2 Probabilities of each species of consuming the blue potato mash. Stars (*) indicate significant differences

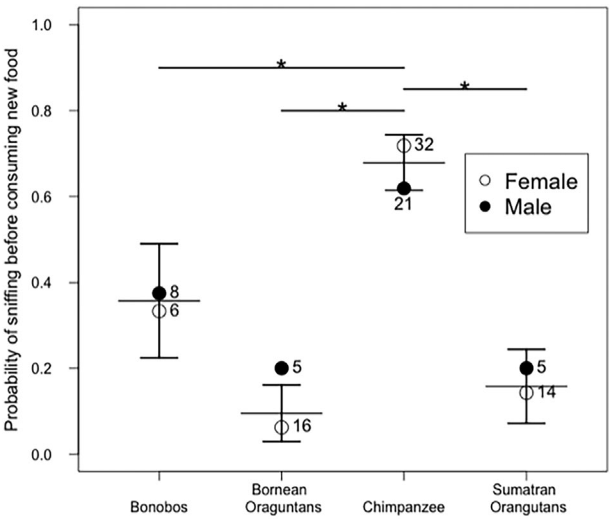

FIGURE 4 Average (longer horizontal middle line) ± SE (shorter horizontal lines) probability of each species of sniffing novel food before consuming it. Numbers indicate sample sizes and stars (*) indicate significant differences. Circles represent the averages of each sex

encounter new food sources in their natural habitats. In general, the probability for a chimpanzee or a bonobo to have access to social information is higher than that for a solitary orangutan. Although, in some chimpanzee populations female sociality is reported to be lower and more like that of some Sumatran orangutan populations (Pusey & Schroepfer-Walker, 2013), in our data we could not identify any sex difference in novelty response in chimpanzees. Thus, besides gregariousness, additional factors can be expected to influence how the different apes respond to novelty. Due to high competition, chimpanzees and bonobos need to be highly responsive to the activity of conspecifics also outside the feeding context (Kano, Hirata, & Call, 2015; Kutsukake, 2006; Murray, Mane & Pusey, 2007; Palagi, 2006; Stanford, 1998) and thus, selection on social attentiveness is expected to be high. Consequently, chimpanzees and bonobos may be highly tuned to attend to what others do and use that information for their own behavioral reactions.

Furthermore, on a sub-species level, chimpanzees differ in sociality, as *Pan troglodytes* verus is described as more gregarious than *Pan troglodytes schweinfurthii* (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2004). Therefore, to assess the *social information hypothesis* on a smaller phylogenetic scale one would need to test for differences within the genus *Pan*. Unfortunately, this was

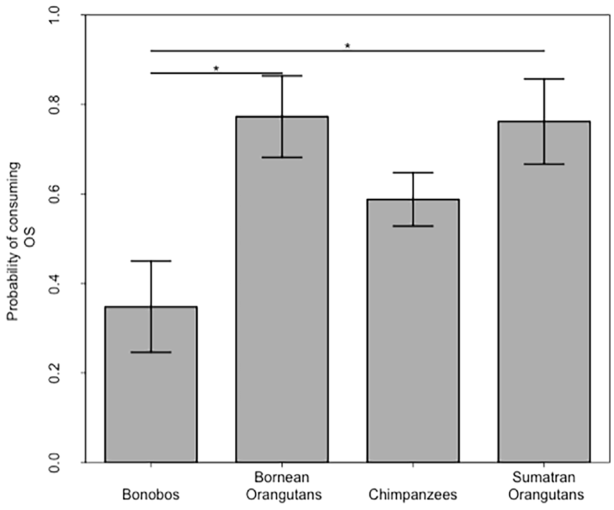

FIGURE 3 Probabilities of each species of consuming the olives. Stars (*) indicate significant differences

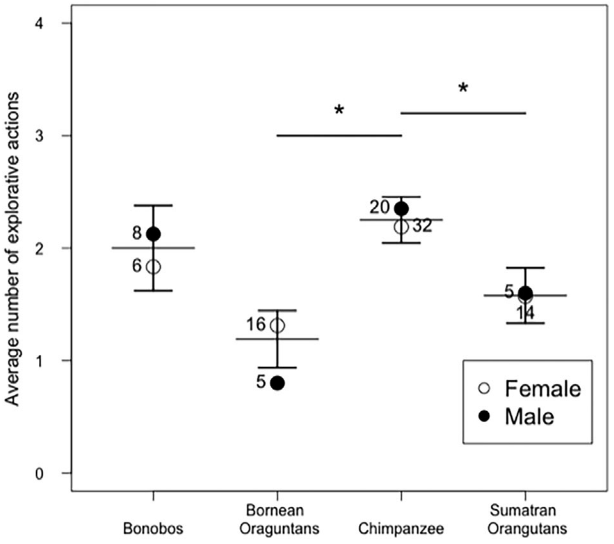

FIGURE 5 Average number of explorative actions (longer horizontal middle line) ± SE (shorter horizontal lines) performed by each species before consuming novel foods. Numbers indicate sample sizes and stars (*) indicate significant differences. Circles represent the averages of each sex

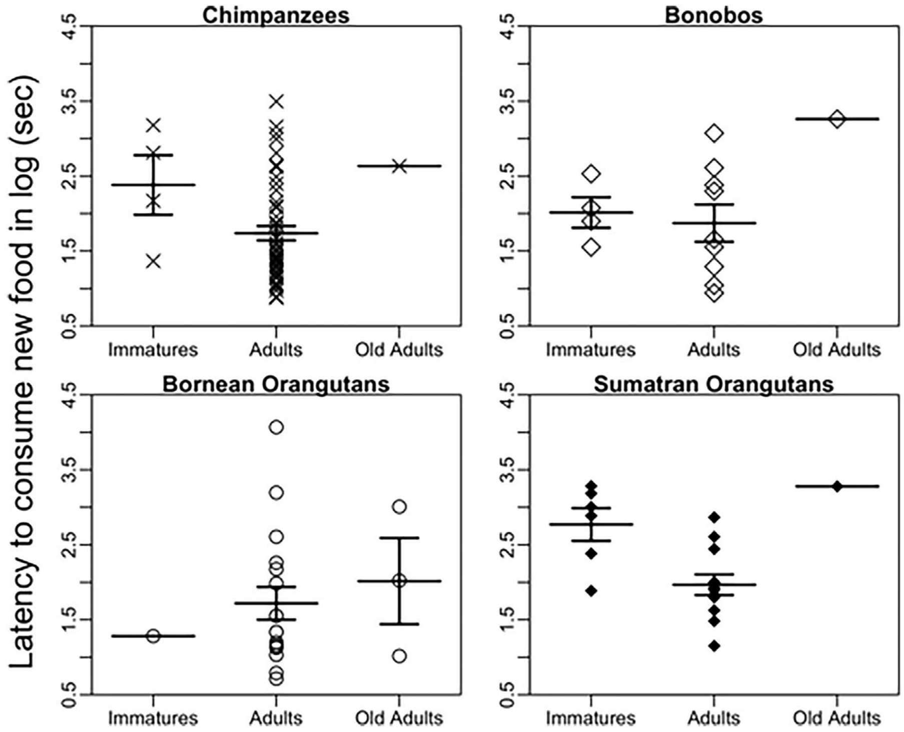

FIGURE 6 Average latencies ± SE to consume novel foods by the three age classes of each species of great ape

not possible in our study as we did not have clear groups representing both sub-species and some individuals in captive facilities were suspected to be hybrids. Subtle differences in neophobia exist between the orangutan species, as the more gregarious Sumatran orangutans have been found to be more cautious than their Bornean relatives (Forss et al., 2016). However, these results controlled for rearing effects where only mother-reared individuals with close to similar experiences were tested. As rearing backgrounds and human related experiences also influence how individuals respond to novelty (Damerius et al., 2017; Damerius, Graber, Willems, & van Schaik, 2017), it would be interesting if future studies would acknowledge such experience effects within and across species.

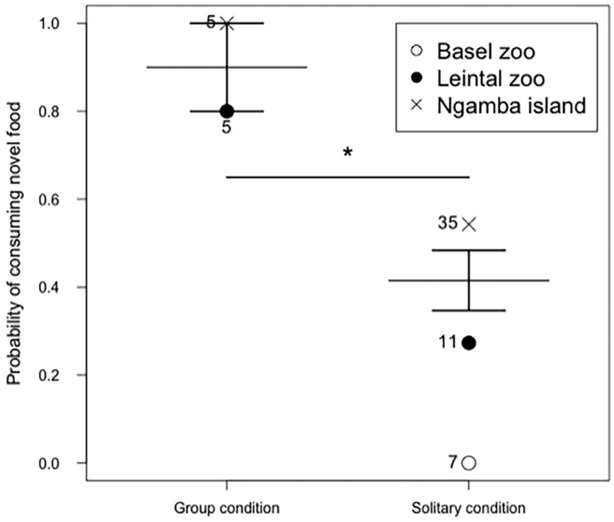

FIGURE 7 Average probabilities (longer horizontal middle line) ± SE (shorter horizontal lines) to consume novel food by chimpanzees in single and group condition at three facilities. Numbers indicate sample sizes and the star (*) indicates significant differences

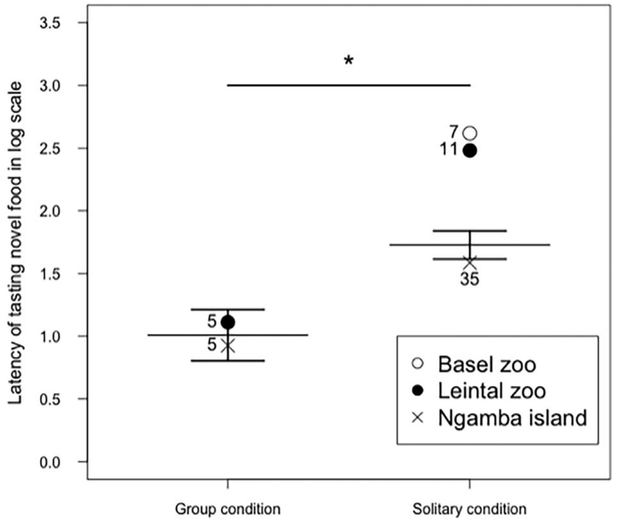

FIGURE 8 Average latency to taste novel food (longer horizontal middle line) ± SE (shorter horizontal lines) of chimpanzees in group and single condition at three testing facilities. Numbers indicate sample sizes and the star (*) indicates significant differences

As the life history pace of orangutans is somewhat slower than the other great apes, one would expect higher neophobia in orangutans. However, such result was not manifested in our data. Instead, our data suggests general ontogenetic differences within species, as out of those individuals who *did* taste novel food items, age classes differed in the latency to taste novel food, while species did not. Adults were significantly faster at tasting novel food than both immatures and older adults (Figure 6). Until weaning and departure from their mothers, all great apes are constantly in the presence of a major social information source—their mother—that is influencing the acquisition of each individual's diet (Jaeggi, van Noordwijk, & van Schaik, 2008; Schuppli, Meulman, et al., 2016). Consequently, great ape juveniles in general seem to be hesitant and more careful than adults when they are facing novelty alone. In long-lived species, higher neophobia is adaptive in immatures if social information is abundant and before diet proficiency is reached. Our results also agree with findings of apes tested in a social context showing that young subjects are the ones observing others more frequently compared to the other age classes (Gustafsson et al., 2014). On the one hand, our result goes against the idea of a plasticity window in younger individuals, described as a period until the age of five years, during which immatures can more easily learn, or switch foraging techniques compared to adults (Matsuzawa, 1999; Gruber, 2016). In our study, the presented food items did not require any processing, but the possibility remains that flexibility in food manipulation techniques may be different between younger and older individuals and does not reflect food neophobia as such. Adult apes that have spent their whole life in captivity may also have gained more experience and familiarity towards any food item provided by humans compared to younger infants (Damerius et al., 2017) and therefore be less hesitant to taste it. Older adults on the other hand, may be less motivated to explore, as it was found to be the case in macaques (*Macaca sylvanus*), where individuals over 24 years would interact less with novel objects (Almeling et al., 2016).

Our results suggest that species also differed in their explorative actions. We considered explorative actions such as touching, poking and sniffing (prior to tasting the food) to be indicators of both caution and curiosity, as these two traits combined are believed to express behavioral flexibility and innovativeness (Forss et al., 2017; Sol, Timmermans & Lefebvre, 2002; Reader, 2015). In contrast, individuals that directly tasted the novel food items without exploration were regarded as less careful and less explorative. Chimpanzees were in general more cautious and performed more explorative actions before deciding to taste the novel foods than both orangutan species did (Figures 4 and 5). Social information may be an important factor regarding what in the environment to attend to. This would allow individuals to effectively explore and individually assess the edibility of unfamiliar food, which would select for high exploration tendency and curiosity (Damerius et al., 2017; van Schaik et al., 2016), as suggested by the abovementioned sniffing behavior in chimpanzees. Hence, individual exploration tendency may be more pronounced in species that, perhaps, often learn skills socially (Heyes, 2012; Schuppli, Meulman, et al., 2016). Sniffing and observation of the mother were also the first responses of infant chimpanzees when encountering various novel foods (Ueno & Matsuzawa, 2005). Similarly, the only study so far deliberately comparing novel food responses between great apes, also reported chimpanzees as the most cautious species when compared to gorillas and orangutans (Gustafsson et al., 2014). Experiments performed in a social setting demonstrated that chimpanzees attended to conspecifics handling novel food items more frequently than orangutans and gorillas did (Gustafsson et al., 2014). Together with our results, these findings follow the prediction of the *social information hypothesis* that the community living chimpanzees, which possess a complex diet shaped by multiple learning mechanisms (Whiten et al., 2009), should be the species more tuned to social information. In the present study, apes faced novel food alone and, in agreement with Gustafsson et al. (2014), when lacking social information, chimpanzees turned to individual exploration and sniffing before making an assessment regarding edibility (Figure 4).

In a sub-sample of chimpanzees, we additionally tested novel food reactions in a group setting. Our results showed that individuals were both more likely to consume novel food and faster at tasting it in a social condition compared to when they were alone (Figures 7 and 8). This social effect may be due to the informative signals from conspecifics sniffing and tasting the food first. This conspecifics' "safety" signal could explain why the food acceptance was higher in the social condition. However, low latencies would also be expected if chimpanzees behaved according to increased competition in the group setting. In fact, in one of the groups tested, an individual gathered multiple pieces of the novel foods and tried to monopolize them. The other individuals were tolerated close by and showed high interest in the items, which eventually led to all individuals of the group co-feeding on the novel food. Thus, potential competition in the social setting can also lead to low latencies, since also in a competitive group scenario the initial step of attending to the novel food item is influenced by the presence of conspecifics. The same model comparing group versus solitary exposure to novelty also reported significant differences between facilities in the apes' likelihood of consuming the novel foods. The chimpanzees in the three facilities had variable experience with cognitive testing and especially separation from their group members, which may have influenced how cautious they behaved when tested alone. Therefore, we hypothesize that there might be an interaction between facility and testing condition (group or solitary). However, we could not test this hypothesis due to lack of enough data (factors were not completely crossed). As we did not investigate the effect of facility further in this study, future studies should assess how much facility and experience influence traits like exploration and neophobia.

Only 35% of the bonobos consumed the black olives compared to 59% of the chimpanzees and at least 76% in both orangutan species (Table 3). Percentages of consumption were similar for the blue potato mash: bonobos 39%, chimpanzees 46%, Sumatran orangutans 71% and Bornean orangutans 77% (Table 3). Thus, despite the bitter taste supposedly signaling potential harmfulness (Steiner & Glaser, 1984; Steiner et al., 2001), olives were consumed in the same frequency as neutral tasting colored potato mash across species. Most of the tested bonobos were reluctant to taste or consume any of the novel foods (Figures 2 and 3) but with the few who did taste it, we did not find the same significant increase in exploration as in chimpanzees. Thus, lack of sniffing behavior or exploratory actions in the bonobos may reflect the low number of individuals who did *taste* the novel foods compared to a much larger number of chimpanzee tasters. Bonobos are generally described as reluctant, shy and less risk-seeking compared to chimpanzees (Call, 2017; Hare, Wobber, & Wrangham, 2012; Herrmann, Hare, Call, & Tomasello, 2010; Rosati & Hare, 2013; Staes et al., 2016). Thus, as novelty exploration is believed to be part of the expression of temperament in animals (Réale, Reader, Sol, McDougall, & Dingemanse, 2007), our results of higher food neophobia and lower exploration in bonobos than chimpanzees aligns with previous findings. Also, one can speculate that the lower exploration tendency or sniffing behavior in bonobos compared to the chimpanzees may reflect the fact that chimpanzee diets are described as more complex regarding the processing techniques involved (such as multiple forms of tool use) which require a certain level of exploration and practice (Whiten et al., 1999) Therefore exploratory tendencies might have been selected for in chimpanzees.

In conclusion, our comparisons of novel food responses in great apes confirmed clear differences between the *Pongo*- and the two *Pan* species. Food neophobia was less strong in both orangutan species, while bonobos and chimpanzees were more cautious to taste and consume novel foods. We speculate that the observed species differences can result from the different social lives of *Pongo*- and *Pan* species. In general, when exposed to novelty alone, immature individuals, as well as older adults were more hesitant in tasting new foods than adults (Figure 6). Despite learning most of their diet socially (Jaeggi et al., 2010; Schuppli, Meulman, et al., 2016), orangutans expand their home ranges in a solitary manner after weaning and therefore face potential new food sources alone as adults, which may lower their neophobia in comparison to the more social apes. Living most of their time in groups with conspecifics within near distances, bonobos and chimpanzees are not necessarily used to encounter unknown food sources on their own and may thus be especially cautious when exposed to them alone without any social cue to attend to. Chimpanzees explored the food items more thoroughly and sniffed before tasting them (Figures 4 and 5). Factors related to cautiousness such as neophobia and inhibitory control, promote cognitive plasticity and problem-solving skills in apes (Beran & Hopkins, 2018; Damerius et al., 2017, Damerius, Graber, Willems, & van Schaik, 2017; Forss et al., 2016; MacLean et al., 2014; Manrique et al., 2013). However, socially biased neophobia can also be related to prevention of behavioral flexibility leading to conservatism, which in turn hinders innovativeness (Gruber, Muller, Strimling, Wrangham, & Zuberbühler, 2009; Harrison & Whiten, 2018; Hrubesch, Preuschoft, & van Schaik, 2009; Price, Wood, & Whiten, 2017). By addressing both within species plasticity and intraspecific comparisons, future research can hopefully clarify the role of neophobia and cautiousness in the adaptation of new foraging techniques demanding behavioral flexibility.

ETHIC STATEMENT

All novel food tests were non-invasive and solely behavioral observations which complied with the ethical principles and animal husbandry approval of each European study facility. Furthermore, the study was supported by BIAZA, British and Irish Association of Zoos and Aquariums. In Uganda, the study was approved on by the UWA, Ugandan Wildlife Authority (UWA/COD/95/06) and UNSCT, Uganda National Council for Science and Technology.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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REFERENCES

Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, A. M., & Fischer, J. (2016). Motivational shifts in aging monkeys and the origins of social selectivity. *Current Biology*, *26*(13), 1744–1749. https://doi.org/10.1016/j.cub.2016.04.066

Bastian, M. L., Zweifel, N., Vogel, E. R., Wich, S. A., & van Schaik, C. P. (2010). Diet traditions in wild orangutans. *American Journal of Physical Anthropology*, *143*(2), 175–187. https://doi.org/10.1002/ajpa.21304

Baayen, R. H. (2008). *Analyzing linguistic data*. Cambridge: Cambridge University Press, https://doi.org/10.1017/S0305000909990080

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.3389/fpsyg.2013.00328

Beran, M. J., & Hopkins, W. D. (2018). Self-control in chimpanzees relates to general intelligence. *Current Biology*, *28*(4), 574–579. e573. https://doi.org/10.1016/j.cub.2017.12.043

Bergman, T. J., & Kitchen, D. M. (2009). Comparing responses to novel objects in wild baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*). *Animal Cognition*, *12*, 63–73. https://doi.org/10.1007/s10071-008-0171-2

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition*, *6*(4), 213–223. https://doi.org/10.1007/s10071-003-0183-x

Boesch, C. (1995). Innovation in wild chimpanzees (Pan troglodytes). *International Journal of Primatology*, *16*(1), 1–16. https://doi.org/10.1007/BF02700150

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. USA: Oxford University Press.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Boyd, R., & Richerson, P. (1985). *Culture and the Evolutionary Process*. Chicago: The University of Chicago Press.

Call, J. (2017). *Bonobos, chimpanzees and tools: Integrating species-specific psychological biases and socio-ecology*. Bonobos: Unique in Mind, Brain, and Behavior, (p. 171).

Chapman, C. A., White, F. J., & Wrangham, R. W. (1994). Party size in chimpanzees and bonobos. In W. C. McGrew (Ed.), *Chimpanzee Cultures*, pp. 41–58.

Damerius, L. A., Forss, S. I., Kosonen, Z. K., Willems, E. P., Burkart, J. M., Call, J., … van Schaik, C. P. (2017). Orientation toward humans predicts cognitive performance in orang-utans. *Scientific Reports*, *7*, 40052. https://doi.org/10.1038/srep40052

Damerius, L. A., Graber, S. M., Willems, E. P., & van Schaik, C. P. (2017). Curiosity boosts orang-utan problem-solving ability. *Animal Behaviour*, *134*, 57–70. https://doi.org/10.1016/j.anbehav.2017.10.005

Deaner, R. O., Isler, K., Burkart, J., & van Schaik, C. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior and Evolution*, *70*, 115–124. https://doi.org/10.1159/000102973

Dobson, A. J., & Barnett, A. (2008). *An introduction to generalized linear models*. Chapman & Hall Book, CRC Texts in Statistical Science.

Doran-Sheehy, D., Mongo, P., Lodwick, J., & Conklin-Brittain, N. L. (2009). Male and female western gorilla diet: Preferred foods, use of fallback resources, and implications for ape versus old world monkey foraging strategies. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *140*(4), 727–738. https://doi.org/10.1002/ajpa.21118

Forss, S. I., Koski, S. E., & van Schaik, C. P. (2017). Explaining the paradox of neophobic explorers: The social information hypothesis. *International Journal of Primatology*, *38*(5), 799–822. https://doi.org/10.1007/s10764-017-9984-7

Forss, S. I., Schuppli, C., Haiden, D., Zweifel, N., & Van Schaik, C. P. (2015). Contrasting responses to novelty by wild and captive orangutans. *American Journal of Primatology*, *77*(10), 1109–1121. https://doi.org/10.1002/ajp.22445

Forss, S. I., Willems, E., Call, J., & van Schaik, C. P. (2016). Cognitive differences between orang-utan species: A test of the cultural intelligence hypothesis. *Scientific Reports*, *6*, https://doi.org/10.1038/srep30516

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, *65*(1), 47–55. https://doi.org/10.1007/s00265-010-1038-5

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression*. Los Angeles, London, New Delhi, Singapore, Washington DC, Melbourne: Sage Publications.

Furuichi, T. (2009). Factors underlying party size differences between chimpanzees and bonobos: A review and hypotheses for future study. *Primates*, *50*(3), 197–209. https://doi.org/10.1007/s10329-009-0141-6

Giraldeau, L.-A., (1997). The ecology of information use. In J. R. Krebs, & N. B. Davies, (Eds.), *Behavioural ecology: An evolutionary approach*. Australia: Blackwell Publishing Company, *Vol. 4*.

Goodale, E., Ratnayake, C. P., & Kotagama, S. W. (2014). Vocal mimicry of Alarm-Associated sounds by a drongo elicits flee and mobbing responses from other species that participate in Mixed-Species bird flocks. *Ethology*, *120*(3), 266–274. https://doi.org/10.1111/eth.12202

Goodall, J. (1986). The chimpanzees of Gombe: Patterns of behavior.

Greenberg, R. (Ed.) (2003). *The role of neophobia and neophilia in the development of innovative behaviour of birds*. Oxford University press.

Gruber, T., Muller, M. N., Strimling, P., Wrangham, R., & Zuberbühler, K. (2009). Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Current Biology*, *19*(21), 1806–1810. https://doi.org/10.1016/j.cub.2009.08.060

Gruber, T. (2016). Great apes do not learn novel tool use easily: Conservatism, functional fixedness, or cultural influence? *International Journal of Primatology*, *37*(2), 296–316. https://doi.org/10.1007/s10764-016-9902-4

Gruber, T., & Clay, Z. (2016). A comparison between bonobos and chimpanzees: A review and update. *Evolutionary Anthropology: Issues, News, and Reviews*, *25*(5), 239–252. https://doi.org/10.1002/evan.21501

Gustafsson, E., Saint Jalme, M., Bomsel, M.-C., & Krief, S. (2014). Food neophobia and social learning opportunities in great apes. *International Journal of Primatology*, *35*(5), 1037–1071. https://doi.org/10.1007/s10764-014-9796-y

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), 573–585. https://doi.org/10.1016/j.anbehav.2011.12.007

Harrison, R. A., & Whiten, A. (2018). Chimpanzees (*Pan troglodytes*) display limited behavioural flexibility when faced with a changing foraging task requiring tool use. *PeerJ*, *6*, e4366. https://doi.org/10.7717/peerj.4366

Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PLoS ONE*, *5*(8), e12438. https://doi.org/10.1371/journal.pone.0012438

Heyes, C. (2012). What's social about social learning? *Journal of Comparative Psychology*, *126*(2), 193. http://psycnet.apa.org/doi/10.1037/a0025180

Hladik, C. M., & Simmen, B. (1996). Taste perception and feeding behavior in nonhuman primates and human populations. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *5*(2), 58–71. https://doi.org/10.1002/(SICI)1520-6505(1996)5:2%3C58::AID-EVAN5%3E3.0.CO;2-S

Hrubesch, C., Preuschoft, S., & van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Animal Cognition*, *12*(2), 209. https://doi.org/10.1007/s10071-008-0183-y

Husson, S. J., Wich, S. A., Marshall, A. J., Dennis, R. D., Ancrenaz, M., Brassey, R., … Simorangkir, T. (2009). Orangutan distribution, density, abundance and impacts of disturbance. Orangutans: Geographic variation in behavioral ecology and conservation, 77–96.

Jaeggi, A. V., Dunkel, L. P., Van Noordwijk, M. A., Wich, S. A., Sura, A. A. L., & Van Schaik, C. P. (2010). Social learning of diet and foraging skills by wild immature Bornean orangutans: Implications for culture. *American Journal of Primatology*, *72*(1), 62–71. https://doi.org/10.1002/ajp.20752

Jaeggi, A. V., van Noordwijk, M. A., & van Schaik, C. P. (2008). Begging for information: Mother-offspring food sharing among wild Bornean orangutans. *American Journal of Primatology*, *70*(6), 533–541. https://doi.org/10.1002/ajp.20525

Johnson, E. C. (2007). Rhesus macaques (*Macaca mulatta*) are not neophobic toward novel food with a high sugar content. *American Journal of Primatology*, *69*(5), 591–596. https://doi.org/10.1002/ajp.20364

Kano, F., Hirata, S., & Call, J. (2015). Social attention in the two species of pan: Bonobos make more eye contact than chimpanzees. *PLoS ONE*, *10*(6), e0129684. https://doi.org/10.1371/journal.pone.0129684

Kano, T. (1982). The social group of pygmy chimpanzees (Pan paniscus) of Wamba. *Primates*, *23*(2), 171–188. https://doi.org/10.1007/BF02381159

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *308*(1135), 203–214. https://doi.org/10.1007/BF023811591098/rstb.1985.0020

Kuroda, S. (1979). Grouping of the pygmy chimpanzees. *Primates*, *20*(2), 161–183. https://doi.org/10.1007/BF02373371

Kutsukake, N. (2006). The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology*, *112*(6), 581–591. https://doi.org/10.1111/j.1439–0310.2006.01200.x

Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, *32*(1), 4–14. https://doi.org/10.3758/BF03196002

Lee, Y., & Nelder, J. A. (1998). Generalized linear models for the analysis of quality-improvement experiments. *Canadian Journal of Statistics*, *26*(1), 95–105. https://doi.org/10.2307/3315676

Lehmann, J., & Boesch, C. (2004). To fission or to fusion: Effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiology*, *56*(3), 207–216. https://doi.org/10.1007/s00265-004-0781-x

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models*. CRC press, Vol. *37*.

MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., . . . Barnard, A. M. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences*, *111*(20), E2140–E2148. https://doi.org/10.1073/pnas.1323533111

Manrique, H. M., Völter, C. J., & Call, J. (2013). Repeated innovation in great apes. *Animal Behaviour*, *85*(1), 195–202. https://doi.org/10.1016/j.anbehav.2012.10.026

Masi, S., Asselain, N., Robelin, L., Bourgeois, A., Hano, C., Dousseau, G., . . . Krief, S. (2013). Response to bitter substances in primates: Roles of diet tendency and weaning age. *Cognitive, Affective, & Behavioral Neuroscience*, *13*(4), 916–929. https://doi.org/10.3758/s13415-013-0171-9

Matsuzawa, T. (1999). Communication and tool use in chimpanzees: cultural and social contexts. *The Designs of Animal Communication*, 645–671.

Matsuzawa, T., & Yamakoshi, G. (1996). Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. Reaching into thought: The minds of the great apes, 211–232.

McGrew, W. C., Marchant, L. F., & Nishida, T. (1996). *Great ape societies*. Cambridge University Press.

Mettke-Hofmann, C. (2014). Cognitive ecology: Ecological factors, life-styles, and cognition. *Wiley Interdisciplinary Reviews: Cognitive Science*, *5*(3), 345–360. https://doi.org/10.1002/wcs.1289

Murray, C. M., Mane, S. V., & Pusey, A. E. (2007). Dominance rank influences female space use in wild chimpanzees, *Pan troglodytes*: towards an ideal despotic distribution. *Animal Behaviour*, *74*(6), 1795–1804. https://doi.org/10.1016/j.anbehav.2007.03.024

Nishida, T. (1968). The social group of wild chimpanzees in the Mahali Mountains. *Primates*, *9*(3), 167–224. https://doi.org/10.1007/BF01730971

Nishida, T., Matsusaka, T., & McGrew, W. C. (2009). Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: A review. *Primates*, *50*(1), 23–36. https://doi.org/10.1007/s10329-008-0109-y

Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): Implicationsfor natural social systems and interindividual relationships. *American Journal of Physical Anthropology*, *129*(3), 418–426. https://doi.org/10.1002/ajpa.20289

Price, E. E., Wood, L. A., & Whiten, A. (2017). Adaptive cultural transmission biases in children and nonhuman primates. *Infant Behavior and Development*, *48*, 45–53. https://doi.org/10.1016/j.infbeh.2016.11.003

Pusey, A. E., & Schroepfer-Walker, K. (2013). Female competition in chimpanzees. *Philosophical Transactions of the Royal Society B*, *368*-(1631), 20130077. https://doi.org/10.1098/rstb.2013.0077.

Team, R. C. (2017). R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2017.

Ramsey, G., Bastian, M. L., & van Schaik, C. (2007). Animal innovation defined and operationalized. *Behavioral and Brain Sciences*, *30*(4), 393–407. https://doi.org/10.1017/S0140525×07002373

Reader, S. M. (2015). Causes of individual differences in animal exploration and search. *Topics in Cognitive Science*, *7.3*, 451–468. https://doi.org/10.1111/tops.12148

Reader, S. M., Hager, Y., & Laland, K. N. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *366*, 1017–1027. https://doi.org/10.1098/rstb.2010.0342

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291–318. https://doi.org/10.1111/j.1469–185X.2007.00010.x

Remis, M. (2003). Are gorillas vacuum cleaners of the forest floor? The roles of body size, habitat, and food preferences on dietary flexibility and nutrition. Gorilla biology: A multidisciplinary perspective, 385–404.

Remis, M. (2006). The role of taste in food selection by African apes: Implications for niche separation and overlap in tropical forests. *Primates*, *47*(1), 56–64. https://doi.org/10.1007/s10329-005-0145-9

Remis, M., & Kerr, M. (2002). Taste responses to fructose and tannic acid among gorillas (*Gorilla gorilla gorilla*). *International Journal of Primatology*, *23*(2), 251–261. https://doi.org/10.1023/A: 1013827310497

Reynolds, V., Plumptre, A. J., Greenham, J., & Harborne, J. (1998). Condensed tannins and sugars in the diet of chimpanzees (Pan troglodytes schweinfurthii) in the Budongo Forest, Uganda. *Oecologia*, *115*(3), 331–336. https://doi.org/10.1007/s004420050524

Robson, S. L., Van Schaik, C. P., & Hawkes, K. (2006). The derived features of human life history. The evolution of human life history, 17–44.

Rosati, A. G., & Hare, B. (2013). Chimpanzees and bonobos exhibit emotional responses to decision outcomes. *PLoS ONE*, *8*(5), e63058. https://doi.org/10.1371/journal.pone.0063058

Rozin, P. (1977). *The significance of learning mechanisms in food selection: Some biology, psychology, and sociology of science*. Houston: Baylor University Press.

Russon, A. E., van Schaik, C. P., Kuncoro, P., Ferisa, A., Handayani, D. P., & van Noordwijk, M. A., (2009). Innovation and intelligence in orangutans. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik, (Eds.), *Orangutans, geographic variation in behavioral ecology and conservation*. Oxford New York: Oxford University Press.

Schielzeth, H., & Forstmeier, W. (2008). Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416–420.

Schuppli, C., Meulman, E. J., Forss, S. I., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87–98. https://doi.org/10.1016/j.anbehav.2016.06.014

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041–210X. 2010.00012.x

Sol, D., Timmermans, S., & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour*, *63*(3), 495–502. https://doi.org/10.1006/anbe.2001.1953

Staes, N., Weiss, A., Helsen, P., Korody, M., Eens, M., & Stevens, J. M. (2016). Bonobo personality traits are heritable and associated with vasopressin receptor gene 1a variation. *Scientific Reports*, *6*, 38193. https://doi.org/10.1038/srep38193

Stanford, C. B. (1998). The social behavior of chimpanzees and bonobos: Empirical evidence and shifting assumptions. *Current Anthropology*, *39*(4), 399–420. https://doi.org/10.1086/204757

Steiner, J. E., & Glaser, D. (1984). Differential behavioral responses to taste stimuli in non-human primates. *Journal of Human Evolution*, *13*(8), 709–723. https://doi.org/10.1016/S0047-2484(84)80021-4

Steiner, J. E., Glaser, D., Hawilo, M. E., & Berridge, K. C. (2001). Comparative expression of hedonic impact: Affective reactions to taste by human infants and other primates. *Neuroscience & Biobehavioral Reviews*, *25*(1), 53–74. https://doi.org/10.1016/S0149-7634(00)00051-8

Takahata, Y., Hiraiwa-Hasegawa, M., Takasaki, H., & Nyundo, R. (1986). Newly acquired feeding habits among the chimpanzees of the mahale mountains national park, Tanzania. *Human Evolution*, *1*(3), 277–284. https://doi.org/10.1007/BF02436585

Takasaki, H. (1983). Mahale chimpanzees taste mangoes—Toward acquisition of a new food item?. *Primates*, *24*(2), 273–275. https://doi.org/10.1007/BF02381089

Ueno, A., & Matsuzawa, T. (2005). Response to novel food in infant chimpanzees: Do infants refer to mothers before ingesting food on their own? *Behavioural Processes*, *68*(1), 85–90. https://doi.org/10.1016/j.beproc.2004.09.002

van Schaik, C., Burkart, J., Damerius, L., Forss, S., Koops, K., van Noordwijk, M., & Schuppli, C. (2016). The reluctant innovator: Orang-utans and the phylogeny of creativity. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *371*(1690), in review https://doi.org/10.1098/rstb.2015.0183.

van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates*, *40*(1), 69–86. https://doi.org/10.1006/jhev.1999.0304

van Schaik, C. P., Fox, E. A., & Sitompul, A. F. (1996). Manufacture and use of tools in wild Sumatran orangutans. *Naturwissenschaften*, *83*(4), 186–188. https://doi.org/10.1007/BF01143062

van Schaik, C. P., & van Hooff, J. (1996). Toward an understanding of the orangutan's social system. Great ape societies, 3–15.

van Schaik, C. P., van Noordwijk, M. A., & Wich, S. A. (2006). Innovation in wild Bornean orangutans (*Pongo pygmaeus wurmbii*). *Behaviour*, *143*(7), 839–876. https://doi.org/10.1163/156853906778017944

van Woerden, J. T., Willems, E. P., van Schaik, C. P., & Isler, K. (2012). Large brains buffer energetic effects of seasonal habitats in catarrhine primates. *Evolution*, *66*(1), 191–199. https://doi.org/10.1111/j.1558–5646.2011.01434.x

Visalberghi, E., Valente, M., & Fragaszy, D. (1998). Social context and consumption of unfamiliar foods by capuchin monkeys (Cebus apella) over repeated encounters. *American Journal of Primatology*, *45*(4), 367–380. https://doi.org/10.1002/(SICI)1098-2345(1998)45:4%3C367::AID-AJP4%3E3.0.CO;2-U

Visalberghi, E., & Addessi, E. (2000). Seeing group members eating a familiar food enhances the acceptance of novel foods in capuchin monkeys. *Animal Behaviour*, *60*(1), 69–76. https://doi.org/10.1006/anbe.2000.1425

Visalberghi, E., & Fragaszy, D. (1995). The behaviour of capuchin monkeys, Cebus apella, with novel food: The role of social context. *Animal Behaviour*, *49*(4), 1089–1095. https://doi.org/10.1006/anbe.1995.0137

Visalberghi, E., Yamakoshi, M. M., Hirata, S., & Matsuzawa, T. (2002). Responses to novel foods in captive chimpanzees. *Zoo Biology*, *21*, 539–548. https://doi.org/10.1002/zoo.10057

Voelkl, B., Schrauf, C., & Huber, L. (2006). Social contact influences the response of infant marmosets towards novel food. *Animal Behaviour*, *72*(2), 365–372. https://doi.org/10.1016/j.anbehav.2005.10.013

Webster, S. J., & Lefebvre, L. (2001). Problem solving and neophobia in a columbiform-passeriform assemblage in Barbados. *Animal Behaviour*, *62*(1), 23–32. https://doi.org/10.1006/anbe.2000.1725

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., . . . Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*(6737), 682. https://doi.org/10.1038/21

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*, 2417–2428. https://doi.org/10.1098/rstb.2009.0069

Yamamoto, M. E., & Lopes, F. A. (2004). Effect of removal from the family group on feeding behavior by captive *Callitrix jacchus*. *International Journal of Primatology*, *5*(2), 492–500. https://doi.org/10.1023/B:IJOP0000019164.98756.9c

Yang, H., & Shi, P. (2017). Bitterness Perception in Humans: An Evolutionary Perspective. Bitterness: Perception, Chemistry and Food Processing, 37–50.

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